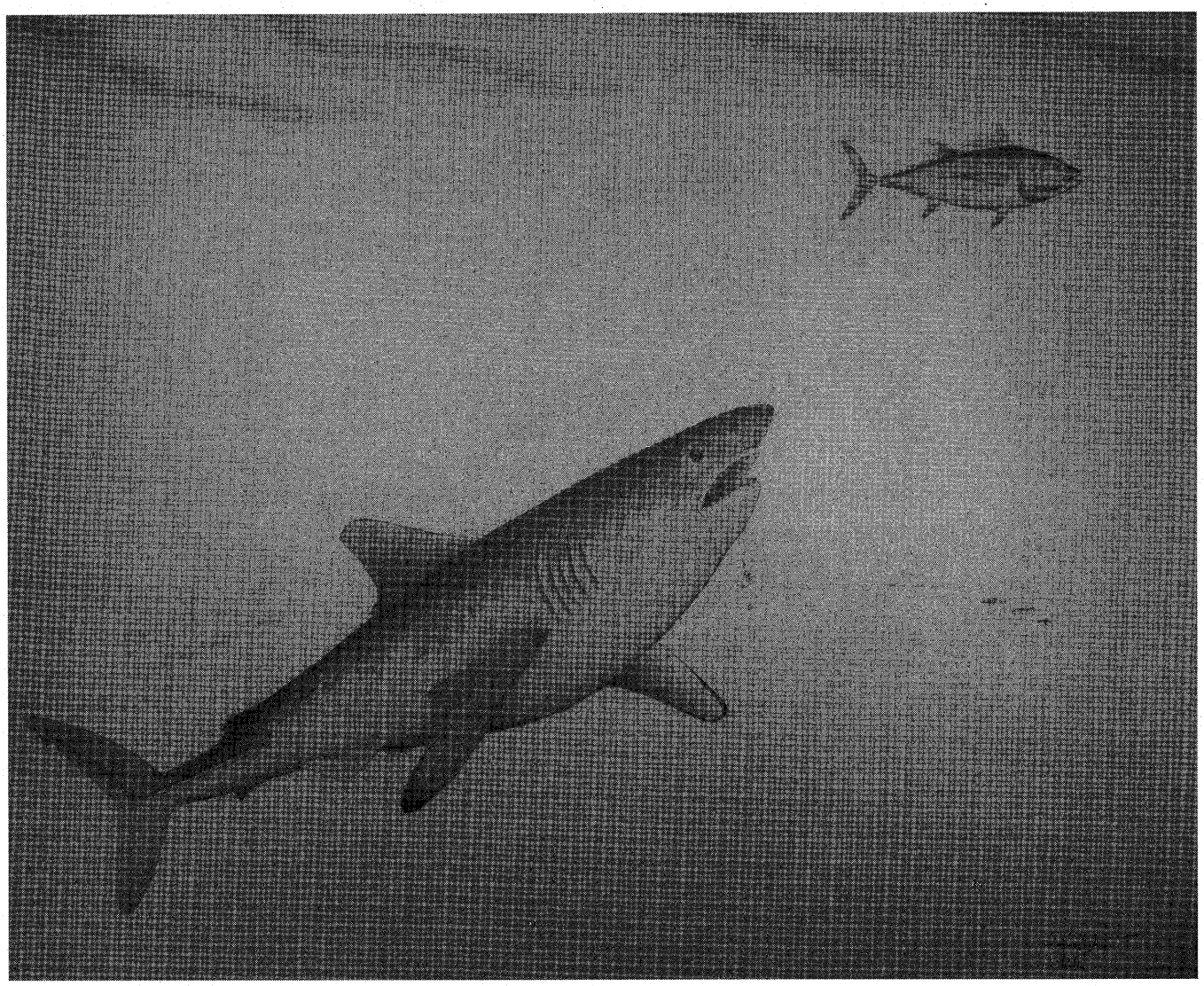
THE MOSASAUR



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COVER ART– "*Parotodus* Stalking Tuna" by David J. Kent.

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A Large Coelacanth, c.f. *Diplurus* (*Pariostegus*) *longicaudatus,* from the Late Triassic Lockatong Formation, Granton Quarry, North Bergen, New Jersey

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ABSTRACT — Five large disarticulated coelacanth bones and a large coprolite were found on a talus slab of gray agrillite (NJSM 15819). The bones consist of an operculum, a cleithrum, a fin ray fragment, a poorly preserved presumptive basisphenoid fragment, and a club shaped bone, possibly a hypobranchial. The agrillite slab was recovered from the north face talus at Granton Quarry in North Bergen, New Jersey. The bones are described and compared with published material. The operculum, cleithrum and fin ray compare favorably with specimens identified as *Diplurus longicaudatus* sensu Schaeffer, a species of rare large fresh water coelacanth. Some inferences on the biology of *D. longicaudatus* and the likelihood that this "species" is a form genus are discussed.

Introduction

Granton Quarry is situated on the northeastern edge of the Newark Basin in North Bergen, NJ. This urban site, an abandoned quarry remnant on the west side of Tonnelle Avenue, is surrounded by industrial properties and the Tonnelle Plaza shopping mall. Granton Quarry sediments, the remains of a large late Triassic lake, have been the source of many important fish and reptile skeletons found and donated to museums by dedicated amateurs as well as professional paleontologists (Olsen, 1980). This paper describes the recent discovery at Granton of disarticulated bones of a large coelacanth fish (NJSM 15819).

Geological Setting

The Newark Basin is the largest of the Triassic - Jurassic rift basins exposed along eastern North America. Collectively known as the Newark Supergroup, the fluvial and lacustrine sediments in these basins are exposed from Nova Scotia to South Carolina and represent 45 million years (Landian/ Carnian to Toarcian) of the rifting which preceded the breakup of Laurasia (Olsen & Flynn, 1989). On the northeastern edge of the Newark Basin, the Granton Quarry site exposes repeated cycles of fossiliferous, predominantly black and gray shales and massive agrillites of the Lockatong Formation. The Lockatong cycles are capped by the Granton sill and underlain by shales and sandstones split by the Palisades sill (Colbert, 1965).

The Lockatong Formation spans the latest middle to early late Carnian (Olsen, 1991). Lockatong deposition suggests orbital (Milankovitch) forcing cycles (Olsen, 1980, 1986 and 1991, Olsen and Baird, 1986, Olsen and Flynn, 1989, and Olsen and Van Houten, 1988), with the most obvious cycles of deposition interpreted as Van Houten cycles (Olsen, 1980). Van Houten cycles are 21,000 year lake deposition cycles consisting of three lithological divisions - transgressive, high stand and regressive facies - resulting from deposition in a tropical monsoonal climate modulated by cyclic variations in the earth's orbit (Olsen, 1986 and 1991, and Olsen and Flynn, 1989).

NJSM 15819 was found among Granton's north face talus. However, paint droplets on the slab and nearby construction debris from the building of the adjacent mall indicate that the specimen may have been moved. Even without tracing the slab to a specific location on the quarry wall, the 11 Van Houten cycles at Granton place it within a 200,000 - 300,000 year period 38 - 46 m above the Palisade sill (Olsen, 1980). Eventual complete coring of the Newark Basin with bio-, magneto-, and Milankovitch chrono-stratigraphy at the Van Houten level of resolution (Olsen and Kent, 1990) should allow precise dating of this and other Newark Basin coelacanth specimens and make possible correlation with Triassic - Jurassic basin faunas worldwide.

Description of NJSM 15819

The 25 X 47 cm gray agrillite slab contains vertebrate remains, mud cracks and parallel extensional fractures (Fig. 1). Manual clearing of the hard matrix with small chisels and a dental scraper and further cleaning of the presumed basiphenoid with dilute acetic acid and soft brushes revealed a large coprolite and the following five large bone fragments:

Operculum

The squamosal face of an operculum measuring 6.5 X 7.5 cm was exposed. A ventral portion was missing, apparently due to weathering. The operculum has a relatively smooth, thickened ridge along the nearly straight dorsal and anterior perimeters. The ridge width ranges from 3.0 - 4.0 mm along the posterior dorsal edge to a maximum of 10.0 mm along the preserved portion of the anterior edge. The remainder of the preserved

squamosal surface is heavily ornamented with densely spaced small, predominantly elongate, anteriorly - posteriorly oriented tubercules.

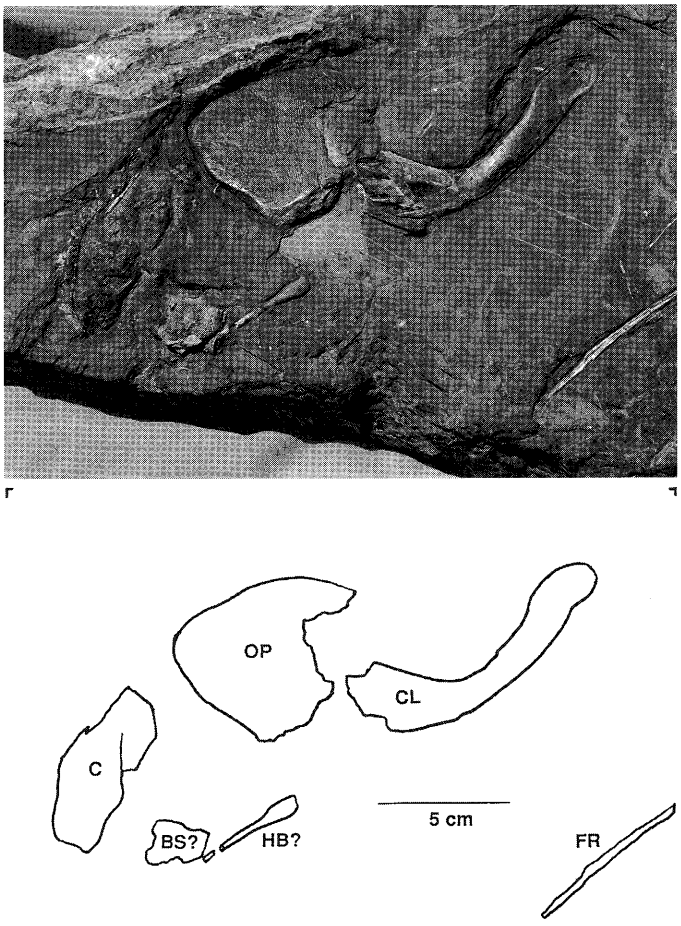

Figure 1. NJSM 15819 photograph (top) and interpretive tracing (bottom). Photograph taken under natural light and at a small angle resulting in slight vertical foreshortening. OP = operculum; CL = cleithrum; FR = fin ray; BS? = presumed basisphenoid; HB? = presumed hypobranchial; and C = coprolite.

Cleithrum

The lateral surface of a cleithrum was exposed. The dorsal portion is complete while the most ventral extension of the lamina is missing. Maximum preserved length is 10.9 cm. The maximum preserved width of the broad, concave, anteriorly extending lamina is 3.5 cm. The dorsal portion, about 1.1 cm wide just above the lamina, flares anteriorly at the dorsal end to produce a rounded, spatulate dorsal terminus 1.6 cm wide. At least three curved ridges parallel the curved dorsal edge suggesting growth lines, a not unexpected finding since "annuli" are present on *Diplurus* scales (Schaeffer, 1952, fig. 12 and pl. 6) and growth lines are found on the scales and some bones of the extant tropical coelacanth *Latimeria chalumnae* (Thomson, 1991).

Fin Ray

Maximum preserved length and width of this fragment are 7.0 cm and 3.0 mm respectively. Approximately 2.0 cm of the preserved length consists of 1.0 mm long segments.

Presumed Hypobranchial

An elongate club - shaped bone 4.1 cm long was exposed. It consists of a broken 2.0 mm wide shaft (circular in cross section with an approximately 0.75 mm diameter filled central hollow) expanding to a 6.0 mm wide X about 1.0 cm long "head".

Presumed Basisphenoid

Adjacent to the club - shaped bone is a badly worn 1.9 X 2.2 cm half ring - shaped bone fragment with two worn, rounded, dorsal(?) protuberances. This bone fragment was already largely exposed when the slab was found, accounting for its eroded condition.

Coprolite

An elongate coprolite containing bone and scale (*Diplurus newarki?*) fragments was exposed. Maximum dimensions (not including folded over portion) are 2.7 x 6.5 cm.

Discussion

Identity and taxonomic assignment of the bones on NJSM 15819

Schaeffer (1948 and 1952) assigned all the large Newark Supergroup coelacanths to the species *Diplurus longicaudatus*, and this trend has continued in the literature (e.g. Murry, 1986) with recent exceptions (e.g. Olsen and Flynn, 1989). A detailed description of the Newark Supergroup genus *Diplurus* and the taxonomy and diagnoses of the only species, *D. longicaudatus* and *D. newarki*, are found in Schaeffer, 1952. Schaeffer (1952) identifies *Diplurus* by a variety of characters including: opercular ornamentation and shape (roughly triangular with near straight dorsal and anterior and curved posterior perimeters); partially segmented and unbranching fin rays; the presence of a narrow cleithrum with a large anterior-medially directed ventral lamina; and a basisphenoid with an ovoid corpus and large, divergent antotic processes. Schaeffer (1952) tentatively supports separate species status for *D. longicaudatus* and *D. newarki* by relative rarity of the former, non-overlapping size ranges (under 20 cm for *D. newarki* vs 69 cm for the complete type *D. longicaudatus* specimen AMNH 630), overlapping but dissimilar stratigraphic and geographic ranges, and heavy opercular ornamentation in *D. longicaudatus* only.

Relative proportions of the bones on NJSM 15819 (Fig. 1) suggest a single large fish as their source. If the identifications of the presumptive basisphenoid fragment and hypobranchial are correct, all the bones except the fin ray can be confidently traced to the posterior skull/pectoral area of a large coelacanth-like fish. The rarity of such fish in Lockatong sediments makes it unlikely these bones represent a taphonomic assemblage from more than one individual.

The Fig. 1 operculum, cleithrum, and fin ray compare favorably with Schaeffer's (1952) descriptions and figures of specimens referred to *D. longicaudatus*, especially PUGM 14955 (Schaeffer, 1952, pl. 15). Using reconstructed proportions for *D. newarki* (Schaeffer, 1952, fig. 9), preserved NJSM 15819 cleithrum and anterior-posterior operculum lengths indicate a minimum estimated body length of about one meter, longer than the *D. longicaudatus* type.

Based on a basisphenoid reconstruction for *D. newarki* (Schaeffer, 1952, fig. 3), the weathered half-ring shaped bone in Fig. 1 suggests a lateral view of a basisphenoid corpus fragment. The "protuberances" may represent worn bases of one of each pair of dorsal basisphenoid projections: the antotic processes and posterior knob-like structures.

The club-shaped bone in Fig. 1 is suggestive of a hypobranchial (see diagrams of gill arch elements of the primitive paleoniscoid *Mimia* and the sarcopterygians *Eusthenopteron* and *Glyptolepis* in Carroll, 1988, figs. 6-12b, and 8-8a and b) and if so, to this writer's knowledge it is the first evidence of this gill element in Newark Supergroup coelacanths.

In light of the above evidence, the NJSM 15819 operculum, cleithrum, fin ray, and presumed basiphenoid fragment fit comfortably within the species *Diplurus longicaudatus* sensu Schaeffer. Evidence, however, now suggests this "species" to be a form genus. Using Schaeffer's criteria, rare examples are reported from two restricted (1-2 million year duration) ranges in the Newark Supergroup sediments (Fig. 2), an older occurrence in late middle to early late Carnian Deep River, Dan

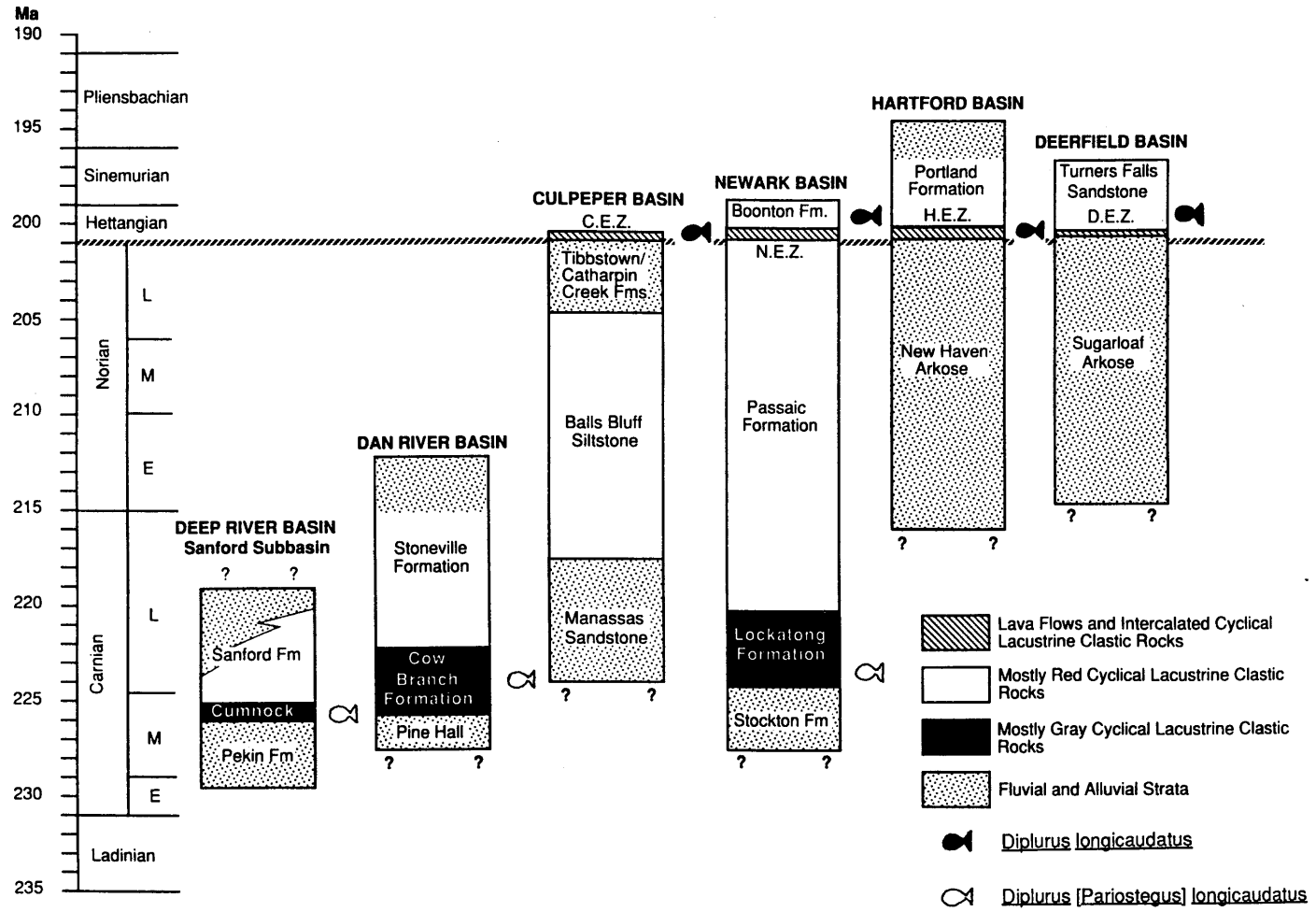

Figure 2. Distribution of large coelacanths in Newark Supergroup rocks. Correlation and facies data of selected Newark Supergroup basins adapted from Olsen (1991, fig. 3). *Diplurus longicaudatus* occurrences as reported by Schaeffer (1948 and 1952), Murry (1986), and P.E. Olsen (Pers. Comm.). Large coelacanth specimens from Newark Jurassic extrusion zone (E.Z.) interflow sequences come from: Culpeper Basin, Midland Formation; Hartford Basin, Shuttle Meadow Formation and East Berlin Formation.

River, and Newark Basin sediments and a younger occurrence (which includes the type AMNH 630) in Hettangian Culpepper, Newark, Hartford and Deerfield Basin sediments (Schaeffer, 1952, Murry, 1986, and P.E. Olsen, Pers. Comm.). These occurrences straddle a 25 million year period of late Triassic marine and terrestrial mass extinctions and a terrestrial faunal turnover which included the radiation of modern tetrapod groups and the dinosaur's rise to Mesozoic dominance (Benton, 1991). Schaeffer's photographs of specimens from each of these large coelacanth occurrences - PUGM 14955 from the Carnian and USNM 18476 from the Hettangian (1952, pls. 15 and 16-2) - show differences in opercular ornamentation and gular shape. Olsen has noted differences in skull bone ornamentation as well and suggests that large Carnian Newark Supergroup coelacanths, including NJSM 15819, are a separate species and should probably be referred to *Pariostegus* (P.E. Olsen, Pers. Comm.).

Some inferences on the biology of *D. longicaudatus* sensu Schaeffer

Studies of the large living coelacanth *Latimeria* show it to be a member of a unique vertebrate superorder. Its hinged skull, reptile-like gular plates, and limb-like paired pectoral and pelvic lobe fins (Smith, 1956) suggest a sister group of the line leading to land vertebrates. Unmistakable coelacanths are recognized as early as the Devonian, and their lineage has changed less than any other known vertebrate line (Smith, 1956). As there have been no changes of importance to general coelacanth evolution since the Triassic (Schaeffer, 1952), *Latimeria* serves as a useful model when attempting inferences on the biology of large Triassic-Jurassic coelacanths (Fig. 3).

Are *D. newarki* the young of large Newark Supergroup coelacanths? The diminutive and often abundant *D. newarki* is reported from the Pekin, Cumnock, Lockatong and Cow Branch Formations (Schaeffer, 1952 and Murry, 1986), a range approximately equivalent to that of the large Carnian Newark Supergroup coelacanth. The absence of similar small coelacanths from Hettangian sediments makes it unlikely that *D. newarki* represents a growth stage of a large coelacanth.

Further evidence is provided by the reproductive biology of coelacanths. All the information we now possess about fossil and living coelacanth reproduction indicates ovoviviparity (Smith et al., 1975), a reproductive strategy unlikely to yield abundant young in a rare species. A 160 cm long female *Latimeria* was found to be carrying in its oviduct five yolk-sac young 30 - 33 cm long (Smith et al., 1975). A second gravid 179 cm long *Latimeria* contained twenty-six 31 - 36 cm long young in its oviduct (Fricke and Frahm, 1992). Finds of large embryos in two fossil coelacanth species (Watson, 1927 and Schultze, 1972) suggest extinct coelacanths had a style of reproduction similar to that in *Latimeria*. Based on the scaling in *Latimeria*, a sexually mature female of the size suggested by NJSM 15819 (about 1m) should have given birth to young at least 17 to 20 cm long, equivalent to the largest *D. newarki* specimens and extending outside the known size range of the species. Finds of isolated scales indicate mature large Carnian Newark Supergroup coelacanths may actually have exceeded 2 m in length (P.E.

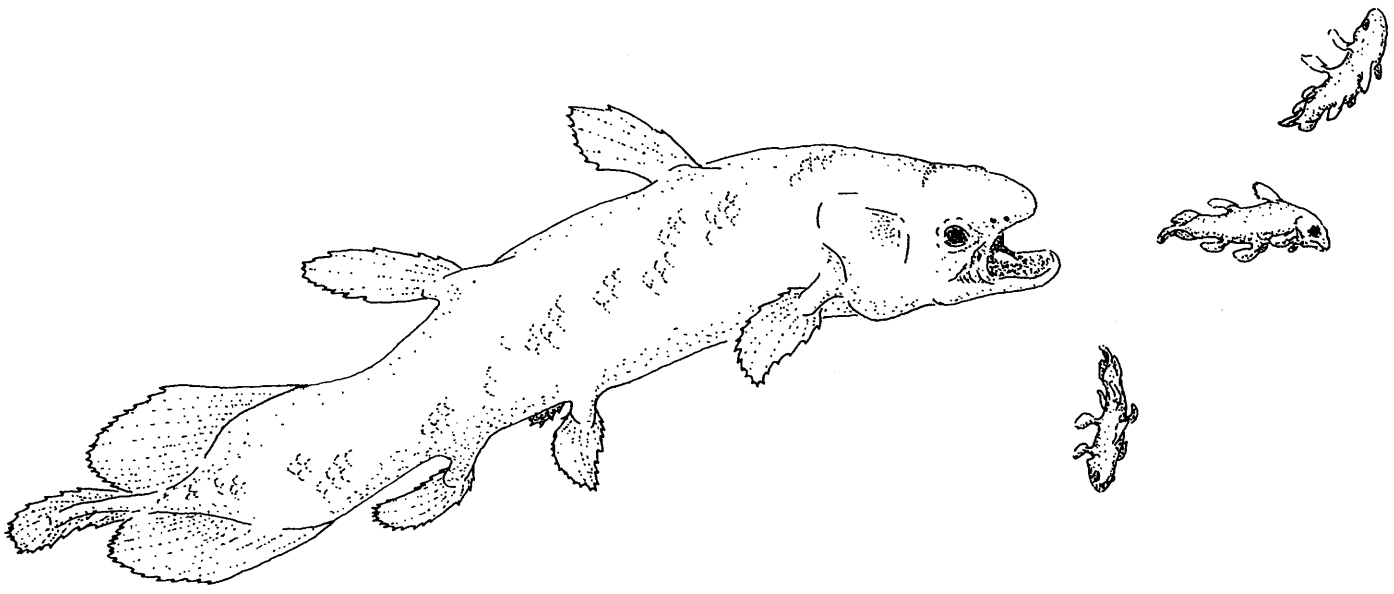

Figure 3. Size and rarity suggest large Newark coelacanths were predators despite their unremarkable dentition. *Diplurus [Pariostegus] longicaudatus* (left) and *D. newarki* (right) depictions based on length inferred from NJSM 15819 and *Diplurus spp.* reconstruction sketches in Schaeffer (1948 and 1952) and Olsen et al. (1982). The extant large piscivorous coelacanth *Latimeria* (K.S. Thomson, 1991) is taken as the model for large Newark Basin coelacanth predatory adaptations, namely use of lobe fins for stealthy approach and combination of powerful caudal fin thrust (H. Fricke et al., 1987) and skull joint, gill apparatus, and jaw adaptations (K.S. Thomson, 1966 and 1991) to effect efficient prey capture.

Olsen, Pers. Comm.). Therefore, *D. newarki* most likely represents a third species of Newark Supergroup coelacanth.

Were Newark Supergroup coelacanths part of a Laurasian coelacanth radiation? A related coelacanth, *Chinlea sorensensi*, is found in the contemporaneous lacustrine and fluvial Dockum Group and Chinle Formation flood plain swamp deposits in Utah, Arizona, and Texas (Murry, 1986). *Diplurus* sensu Schaeffer and *Chinlea* are allied together and separated from all other coelacanths by key characters including basisphenoid shape and long, pleural ribs (Murry, 1986). The presence of this distinct group of coelacanth species in contemporaneous intracontinental drainage basins strongly suggests an evolutionary radiation of fresh water coelacanths occurred in Triassic Laurasia.

Conclusions

NJSM 15819 contains the remains of a large fresh water coelacanth, c.f. *Diplurus longicaudatus* sensu Schaeffer. A need for detailed revision of this species is indicated. Tentatively, NJSM 15819 and similar large Carnian Newark Supergroup coelacanths should probably be referred to the genus *Pariostegus* . In addition, evidence relating to the reproductive biology of extant and extinct coelacanths suggests it is extremely unlikely that *D. newarki* is a growth stage of sympatric large coelacanths and more likely represents a third Newark Supergroup coelacanth species. Critical reevaluation of the remains of Newark Supergroup coelacanths and *C. sorensensi* could reveal even further evolutionary novelty associated with this Triassic fresh water coelacanth radiation.

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Appendix

Institutional abbreviations

AMNH American Museum of Natural History, New York, NY, USA
NJSM New Jersey State Museum, Trenton, NJ, USA
PUGM Princeton University Geological Museum paleontological collection at Yale Peabody Museum, New Haven, CT, USA
USNM United States National Museum, Washington, D.C., USA